Seasonal woody plant shoot growth in *Burkea africana* — *Ochna pulchra* savanna

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Seasonal changes in dry mass of shoots and their leaf and twig components are described for *Ochna pulchra* and *Burkea africana* in a northern Transvaal savanna. Initiation of shoot growth was found to correspond with a higher rate of temperature increase while time of leaf drop appeared to be affected by the rainfall of the current growth season. Later flushes of growth within a given season were relatively uncommon and where they did occur, they were of the order of half the magnitude of the first flush.

Shoot growth per *Ochna pulchra* plant was found to relate to the previous season's rainfall and not to that of the current season of growth. In *Burkea africana*, a similar relation was found, but only for rainfall toward the end of the previous season. From this and other evidence, it appears that shoot growth in these species depends more on carbohydrate reserves than on current photosynthate. The role of pleonanthic and hapaxanthic shoots in affecting relative growth of vegetative shoots per plant between seasons is discussed. Degree of syllepsis in *Ochna pulchra* affects aspects of canopy structure and the interseasonal changes in shoot growth. Plant size was found to relate inversely to individual shoot mass in *Burkea africana* and to relate directly to time of leaf fall in *Ochna pulchra*. Shoot mortality between growth seasons was lower in *Burkea africana* than *Ochna pulchra* and was, in both species, greatest following a season of drought.

S. Afr. J. Bot. 1982, 1: 104 – 116

Seisoensveranderinge in die droëmassa van lote en hul blaar- en stingelkomponente van *Ochna pulchra* en *Burkea africana* in 'n Noord-Transvaalse savanne, word bespreek. Daar is gevind dat die aanvang van lootgroei met 'n hoër tempo van temperatuurstyging saamval terwyl die tyd van blaarval skynbaar deur die reënval van die lopende groeiseisoen beïnvloed word. Latere uitloopsels binne 'n gegewe seisoen is relatief ongewoon en waar dit wel plaasgevind het, was die grootte daarvan omtrent die helfte van dié van die eerste uitloopsels. Daar is gevind dat die groei van lote per plant in die geval van *Ochna pulchra* verband hou met die reënval van die vorige seisoen en nie met dié van die lopende groeiseisoen nie. 'n Ooreenstemmende invloed is op *Burkea africana* waargeneem maar hier was dit slegs dié reënval wat laat in die vorige seisoen geval het wat van belang was. Dit blyk uit hierdie en ander inligting dat die groei van die lote van hierdie plantsoorte waarskynlik meer van koolhidraatreserwes as van pasgevormde fotosintaat afhanklik is. Die invloed wat lote wat eenmaal of meermale per seisoen blom op die relatiewe groei van vegetatiewe lote per plant tussen seisoene het, word bespreek. Die mate van sillepsis in *Ochna pulchra* beïnvloed aspekte van kroonstruktuur en die groei van lote tussen seisoene. Daar is gevind dat die grootte van 'n plant omgekeerd eweredig is aan die massa van 'n individuele loot van 'n *Burkea africana*-plant terwyl dit direk eweredig is aan die tyd van blaarval in die geval van *Ochna pulchra*. Die mortaliteit van lote tussen groeiseisoene was laer by *Burkea africana* as by *Ochna pulchra* maar was vir beide plantsoorte die hoogste na 'n seisoen van droogte.

S.-Afr. Tydskr. Plantk. 1982, 1: 104 – 116

Keywords: biomass, leaf, plant growth, savanna, twig.

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Accepted 14 July 1982

Introduction

'Detailed studies on the periodicity of extension of shoots and renewal of leaves in dicotyledonous trees are surprisingly few' (Hallé *et al.* 1978). Plant shoot production is one of the more important components of vegetation with respect to browse availability in some ecosystems and nutrient cycling, especially in deciduous plant ecosystems. Intra- and interseasonal growth of shoot mass is a measure of the temporal allocation of an important natural resource in many savanna vegetation areas.

A study of seasonal woody plant shoot production was carried out and formed part of a multidisciplinary ecological project in savanna (Huntley & Morris 1978). This project is being undertaken in the Mixed Bushveld Veld Type (Acocks 1975) on the Nylsvley Nature Reserve near Naboomspruit in the northern Transvaal. The dominant woody plant species of the study area are *Burkea africana* and *Ochna pulchra* which are deciduous, generally unpalatable to wild ungulates and comprise two thirds of the total aboveground woody plant biomass of the study site (Rutherford 1979a). The shoots of these species are illustrated in Figure 1. The study area is gently undulating, has sandy soil often more than one metre deep and a mean annual rainfall of 622 mm, of which more than 90% falls between October and April.

Our aims are to:

- describe intraseasonal shoot mass change in *Burkea africana* and *Ochna pulchra* for one season (12 months, July to June);
- compare the shoot growth of the main study season with that of three other seasons, and
- attempt to relate growth patterns with available climatic data.

Methods

Selection of study materials

A 1-ha study plot was selected which satisfied the following criteria: close proximity to the site's weather station; representative plant species composition according to Coetzee *et al.* (1976); full range, proportionately weighted, of tree sizes for the common woody plant species in terms of plant height and stem diameter. Ten individuals were selected for each of the two dominant species, *Burkea africana* and *Ochna pulchra*, with plant heights between two and eight metres and between one and five metres respectively. Similar sample intensities were used for the

Figure 1 (A) Young unbranched vegetative shoot of *Ochna pulchra*, (B) Two young inflorescences of *Ochna pulchra*, (C) Young vegetative shoot of *Burkea africana*, (D) Young *Burkea africana* shoot with inflorescence and bi-pinnately compound leaves.

next two abundant species, *Terminalia sericea* and *Grewia flavescens*, but extreme spatial and temporal variability in shoot growth of these species made their data statistically unsatisfactory for comparison with data for the dominant species. Problems encountered with *Terminalia sericea* were: high mortality of whole branches; staggered initiation of shoot growth mainly from October to December; and conversion to mass of different articulated shoot growth units. In *Grewia flavescens* high mortality of plant parts, sporadic shoot flushing at different times of the year and integration of canopy and basal shoot data, posed special difficulties. Consequently, this paper is limited to the study of the two dominant woody species of the study site. The study started in mid 1976 and ended in December 1979 with the main study season in 1977/78. Annual rainfall totals for the seasons 1976/77, 1977/78, 1978/79 and 1979/80 were 619,3; 791,1; 430,8 and 790,5 mm respectively.

Main study season (1977/78)

To overcome the common problem of bias towards selecting the more obvious individual shoots in savanna tree canopies, measurement zones were used. A measurement zone encompassed all parts of a branch distal to a point on the branch axis approximately two years old and included at least six terminal buds. This point was prominently marked with a plastic tag. The number of measurement zones per plant varied between five and ten according to plant size and were randomly selected in the plant canopy. Scaffolding and ladders alongside the taller trees facilitated access to the upper parts of the canopies. All developing shoots in the measurement zones were tagged below the previous season's bud scars, using numbered, small plastic tags and thin-gauge wire. Sample sizes in this measurement season were 468 shoots for *Ochna pulchra* and 362 for *Burkea africana*. A small paint spot was positioned close

to the bud base of each shoot to serve as permanent shoot length reference point. Measurements taken on each shoot were: shoot length to nearest millimeter with caliper; twig base diameter to nearest 0,1 mm with vernier caliper; number of leaves; branched/unbranched status; and flowering/fruiting recordings. Shoots too young for dimensions to be measured and for leaves to be counted were recorded as juvenile. Also in the first few weeks of growth, the nature of the expanding shoots often precluded diameter measurement and leaf counts and allowed only measurement of shoot length. Each reference paint spot to bud scar distance was determined and subtracted from all length measurements of each shoot. Measurements were taken from the first week of shoot growth activity at weekly intervals for the first six weeks, again at eight weeks, thereafter at approximately four-week intervals for the remainder of the one-year period.

A separate set of at least 30 shoots of each shoot type and plant species were destructively sampled immediately following each of the above-mentioned non-destructive measurement periods. The destructively sampled shoots were taken in the same area from other trees with shoots at a similar stage of development as those on the regularly monitored trees. The destructive measurements were required to parallel the non-destructive measurements for conversion of the latter to mass units for different periods of the season. Shoot growth expressed in terms of only shoot length and diameter is a less sensitive measure of growth than shoot mass which accounts for changes in density of materials and for loss of shoot parts. Percentage change in shoot dimensions also cannot be used to scale directly to other available mass data such as shoot mass per unit ground area. Destructive sampling entailed clipping each shoot at the current season's bud scar marks and measuring each shoot for the above-mentioned parameters. In addition, area of fresh leaves was determined using an electronic planimeter and the shoots were dried to constant mass at 85 °C for determining the dry mass of twig and leaf material. The petiole of the compound leaf of *Burkea africana* was included in the area determination.

Other study seasons

In the other three study seasons, fewer measurements were taken than in the main study season. In the first study season (1976/77) sampling frequency was similar to that in the main study season but shoot sample size was only about 10% on only seven of the ten trees of each species. Area of tagged leaves of *Burkea africana* was measured directly on the tree using an electronic leaf area scanning head. This method was discontinued in subsequent seasons because it was found impracticable for use on juvenile leaves.

In the third study season (1978/79) the measurements of the main study season were repeated in the same measurement zones. All new shoots in these zones were tagged in the same way. Measurements were taken only twice, namely, two and six months after start of growth.

In the fourth and last season (1979/80) the same procedure as in the third season was followed except that the shoots were measured only once, namely three and a half months after start of growth. Only shoot length and twig base diameter were consistently measurable owing to large-scale defoliation by insects of both study species. Since this defoliation commenced after shoot expansion was virtually complete, data for this season were considered comparable with those of the previous seasons.

Computations

Shoot dimensions were related to the mass of various shoot components and the whole shoot by means of least square regressions. Various workers, cited in Rutherford (1979b) have found that shoot dimensions are useful predictors of the mass of shoot components. Shoot length with and without twig diameter was related to twig, leaf and shoot mass using a variety of function types and transformations. Branched and unbranched shoots were tested separately for both species. Regressions with consistently high F

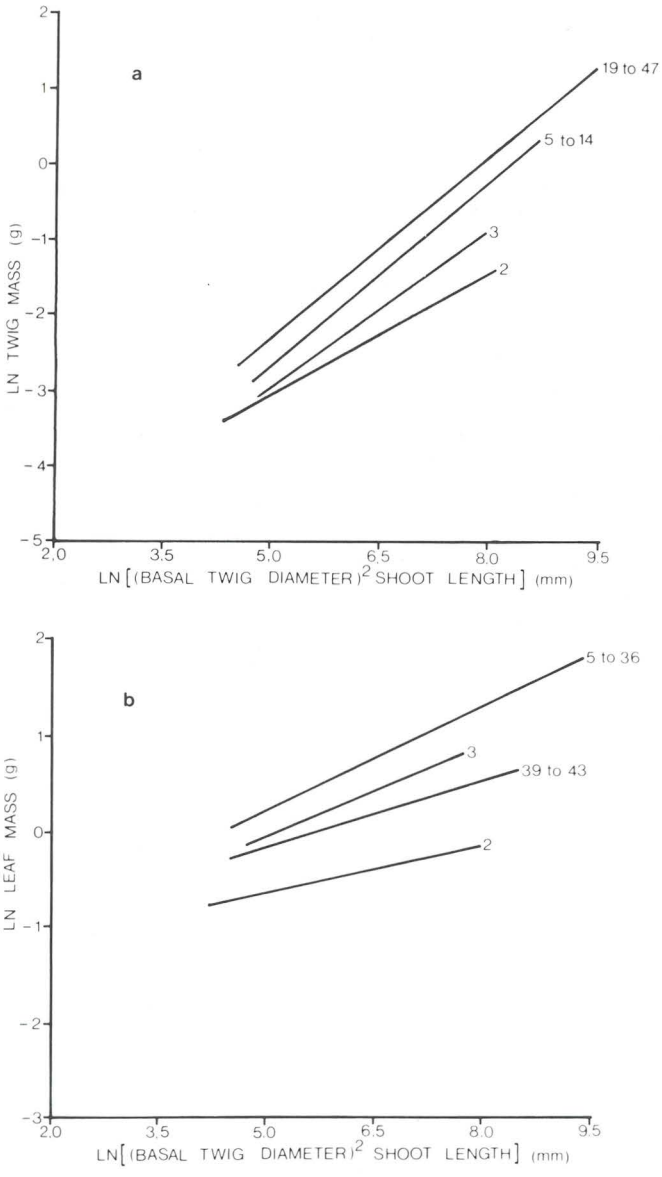

Figure 2 Time dependent regression relations between branched shoot size and (a) dry twig mass and (b) dry leaf mass for *Ochna pulchra* in the main study season. Numerals signify week numbers commencing the first week of September. Formulae for Figure 2a are: week 2, $y = -5{,}7345 + 0{,}5331\,x$; week 3, $y = -6{,}3769 + 0{,}6855\,x$; weeks 5 to 14, $y = -6{,}6999 + 0{,}8071\,x$; weeks 19 to 47, $y = -6{,}3089 + 0{,}7968\,x$. Formulae for Figure 2b are: week 2, $y = -1{,}4390 + 0{,}1614\,x$; week 3, $y = -1{,}6451 + 0{,}3154\,x$; weeks 5 to 36, $y = -1{,}5990 + 0{,}3594\,x$; weeks 39 to 43, $y = -1{,}3059 + 0{,}2276\,x$, where $y = 1n$ (twig or leaf mass in g) and $x = 1n$ (basal twig diameter)^2 (shoot length in mm).

values were selected and linear relations with both the mass category and the shoot dimensions (in the form of basal twig diameter squared and multiplied by shoot length in the same units) logarithmically transformed were found to be most suitable (all significant at $P = 0{,}01$). For periods in which the relations remained constant, data were pooled. In this way a series of time-dependent regression relations between shoot size and various mass categories were derived for each species (for example, Figure 2a, b). Thus for shoots of the same size, twig mass increased or remained constant until the end of the season. Leaf mass increased similarly with regressions but decreased at the end of the season. Since shoots are comprised mainly of leaves, shoot mass regressions displayed a similar pattern to that of leaf mass. Regression formulae were applied to the non-destructive measurements as summarized in Figure 3 using a desktop computer. Requests for copies of the program with the regression coefficient listings may be addressed to the authors. An independent method for determining leaf mass by using leaf counts and mean leaf mass for each measurement period was found to be more sensitive than the above-mentioned regression method for the period of leaf loss. We therefore used the more sensitive method for the latter part of the season. The computer programs for each species were run for individual plants and for groups of plants.

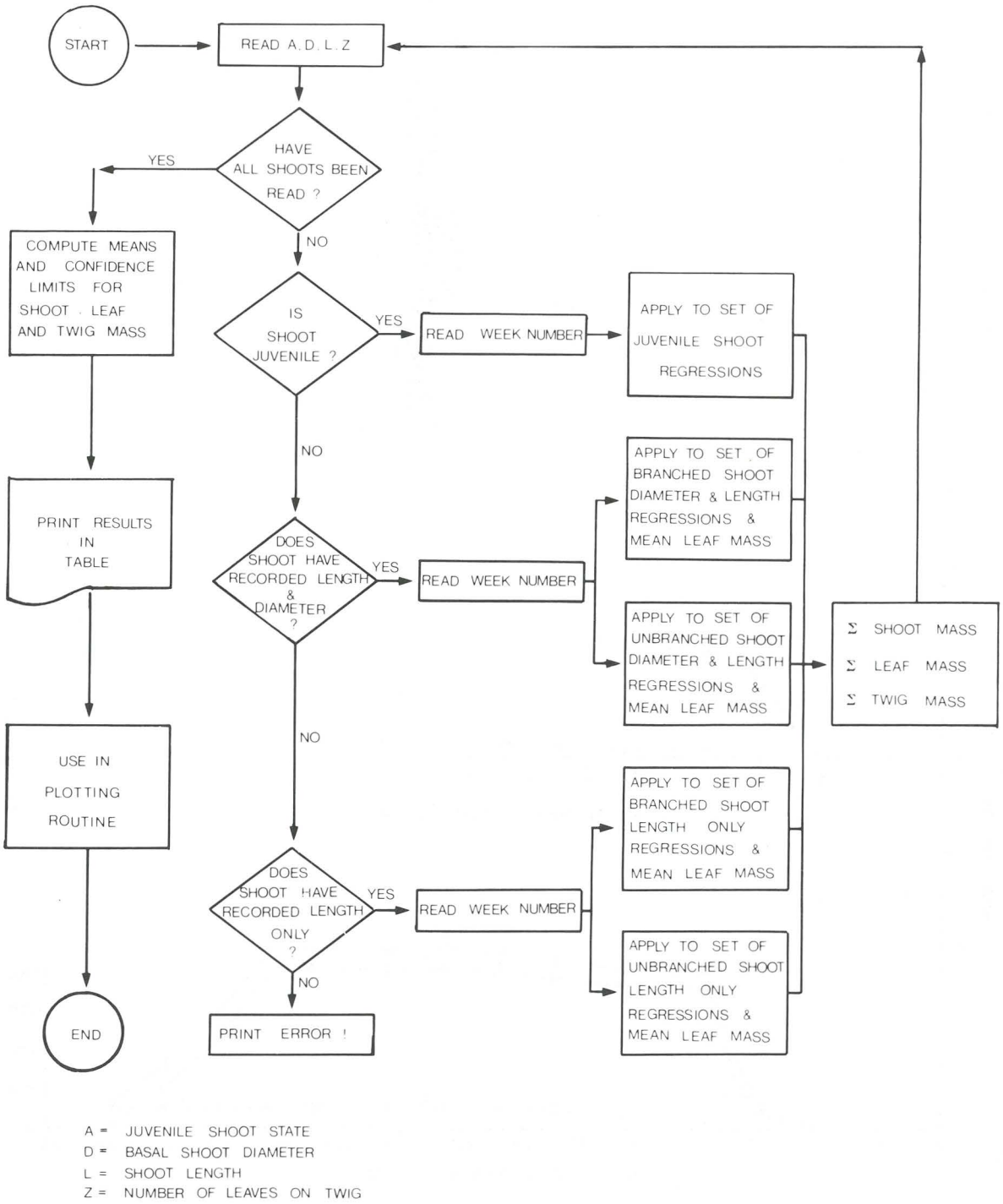

Figure 3 Flow diagram of the program used to convert shoot dimensions to time dependent shoot mass categories for *Ochna pulchra*.

Certain small irregularities sometimes occurred in the expressed growth patterns of both species in the early part of the season. These were caused by: greater variability in regressions involving shoot length only; abrupt change from regressions using length only to those including twig diameter; and the independent calculation of shoot mass from leaf and twig mass resulting in leaf and twig mass not always precisely equalling shoot mass. Largely because of the last-mentioned problem, leaf and twig mass are not plotted separately for the first part of the season.

Specific Leaf Area was calculated by dividing the area of fresh leaves by dry mass of the leaves and was expressed in $cm^2\ g^{-1}$.

For comparison between seasons the sum of the mass of all shoots in all measurement zones was used. This approach allowed for the net effect of new individual shoot growth, shoot survival and recruitment, and branch mortality. Mean shoot size alone or only shoot numbers are insufficient since total growth must account for both changes in shoot mass and in shoot numbers. The method of shoot selection used was similar to that of Halls & Alcaniz (1972) except that in the present study, the same measurement zones were retained to enable comparison of integrated shoot growth between different seasons to be made. The present approach represents an expanded form of the method used for following canopy dynamics by Maconochie & Lange (1970). An alternative method, used by Wilson (1966), where shoot quantities are related to branching order for integration of data over the whole tree, was not employed in the present study. Branching orders in both *Ochna pulchra* and *Burkea africana* are not sufficiently consistent for this purpose. For purposes of standardization, interseasonal comparisons of shoot mass were made for December each year. This resulted in the need for weighted interpolation in the third season and back extrapolation of shoot numbers in the first season.

Results

Intraseasonal growth

Main study season

The seasonal change of shoot, leaf and twig mass is given in Figure 4a for *Ochna pulchra* and in Figure 4b for *Burkea africana*. Shoot growth commenced in the first week of September with most shoot growth occurring within the first eight weeks in both species. This was followed by a period of slight increase over about 26 weeks in *Ochna pulchra* but 31 weeks in *Burkea africana*. Thereafter there was a period of rapid decrease of shoot mass in *Burkea africana* lasting 11 weeks until almost no leaves remained. The corresponding decrease in *Ochna pulchra* was more gradual and leaf loss continued for about 20 weeks. Although change in shoot mass followed that of leaf mass, twig mass remained generally constant after completion of growth in both species. Shoot mass peaked at 1,52 g/shoot in *Ochna pulchra* and at 9,72 g/shoot in *Burkea africana*, that is a six-fold difference. Initiation of leaf emergence in both *Ochna pulchra* and *Burkea africana* anteceded a period of maximum rate of increase in daily temperature and a maximum range of daily temperature (Figure 5). Main period of bud opening in both species corresponds to a photoperiod of between 11,6 and 12,0 h with a weekly rate of increase of about 10 min shortly before the time of the vernal equinox. Observations in some other seasons have indicated that cold snaps in early spring (September) can, however, delay bud opening. The period of maximum shoot expansion corresponded with the period when leaf temperatures were highest ($\approx$ 40 °C) and about twice as much above ambient temperature than later in the

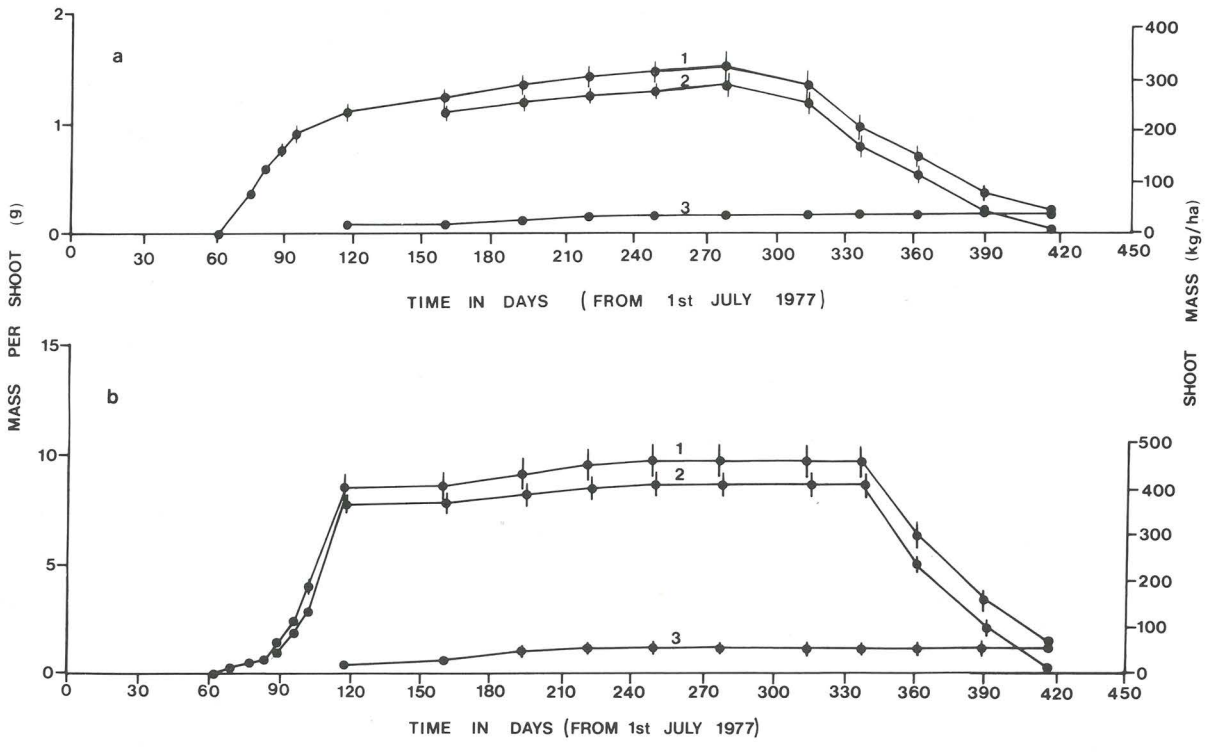

Figure 4 Seasonal change in shoot mass components for (a) *Ochna pulchra* and (b) *Burkea africana* shoots in the main study season where 1 is shoot mass, 2 is leaf mass and 3 is twig mass. 95% confidence limits are indicated. (Mass per unit ground area scaled from Rutherford, 1979a).

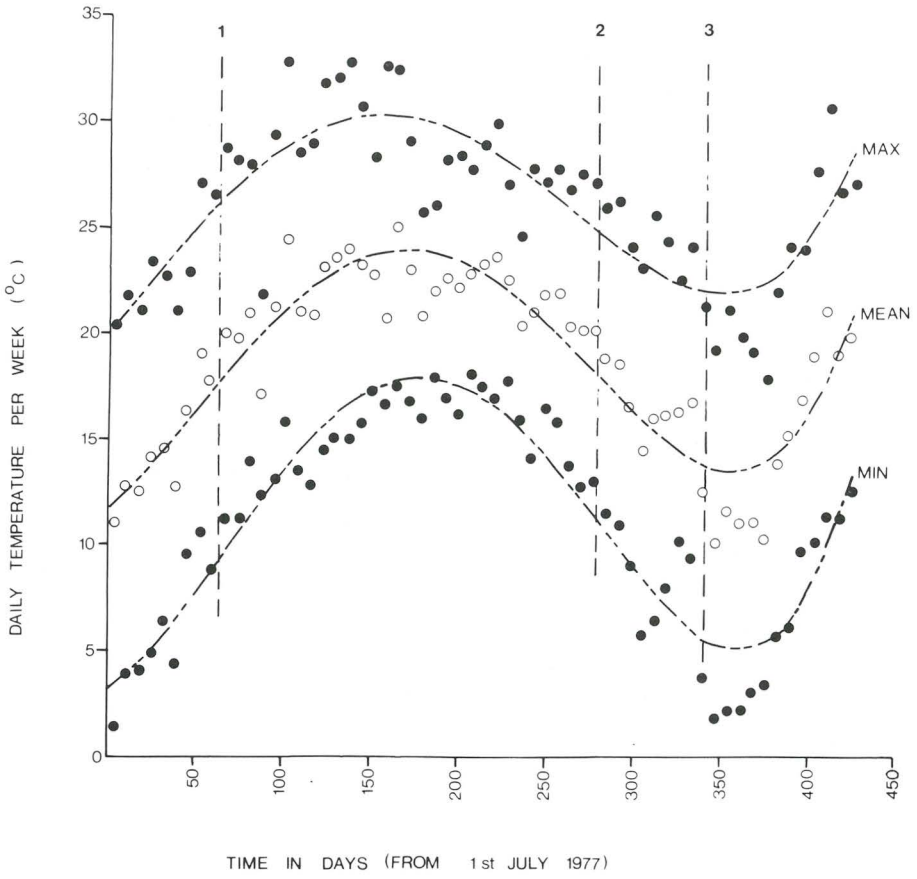

Figure 5 Seasonal change in mean, maximum and minimum daily temperature per week with fitted fourth degree polynomial functions. The earliest set of three values are the minima for winter of 1977. (1) Initiation of leaf emergence in *Ochna pulchra* and *Burkea africana*. (2) Initiation of leaf fall in *Ochna pulchra*. (3) Initiation of leaf fall in *Burkea africana*.

season (Ferrar, pers. comm.).

A significant difference ($P = 0,05$) was found between the seasonal growth of the respective shoot mass categories of branched and unbranched shoots in *Ochna pulchra* (Figure 6a). Branched shoot mass peaked at more than twice that of unbranched shoot mass. A greater proportion of branched shoots commenced growth earlier than in unbranched shoots. Consequently about three quarters of peak shoot mass was reached by the fifth week in branched shoots but only half by this week in unbranched shoots.

Sporadic second flushes of shoot growth occurred over a number of weeks in a few individuals of both species. Twenty one percent of *Ochna pulchra* and 1% of *Burkea africana* shoots flushed a second time. Of the shoots which did flush a second time, the individual shoot mass in the second flush was 47% of that in the first flush in *Ochna pulchra*, and 40% in *Burkea africana*. In *Ochna pulchra* the second flush could be ascribed more to an increase in twig diameter than in shoot length and leaf number but in *Burkea africana* this was more variable. In *Ochna pulchra* there was some rare overlap between first and second flush generations of shoots in the population.

Shoot mortality after the appearance of leaves (dieback) was sporadic and involved only about 1% of shoots in *Ochna pulchra* and 3% in *Burkea africana*. Time of intraseasonal shoot death was limited to the first half of the season in *Ochna pulchra* and the first quarter in *Burkea africana*.

Shoot growth appeared to be independent of plant size in *Ochna pulchra* and there was remarkable uniformity between plants with respect to unbranched shoot mass. However, in *Burkea africana* there was a significant difference ($P = 0,05$) in twig, leaf and shoot growth between small ($\leq$ 240 mm stem diameter at 200 mm above ground) and large ($>$ 240 mm stem diameter at 200 mm above ground) plant groups (Figure 6b). Mean individual shoot mass peaked at 11,53 g for small plants but only 8,81 g for large plants.

The initiation of leaf loss, expressed as the time at which shoot mass fell to 95% of maximum shoot mass, was found to correlate positively with tree height (correlation coefficient of 0,765 and $P = 0,01$) in *Ochna pulchra*. In *Burkea africana* the pattern of leaf and shoot mass decrease did not correlate with tree height. The two *Burkea africana* trees that dropped leaves earliest (all lost by day 391) were the same two trees with the greatest proportion of shoots with inflorescences (both greater than 93%). Different patterns of leaf mass decrease occurred in *Ochna pulchra* plants. These two basically different end of season patterns of change in shoot mass (Figure 6c) differed greatly from the relatively uniform pattern at the start of the season.

Various data from this measurement season showed variation in vegetative shoot types and components which may be important to future shoot sampling strategy. It was found that the proportion of branched shoots in *Ochna pulchra* differed according to position in the canopy. Thirty percent of shoots in the upper half of the canopies were

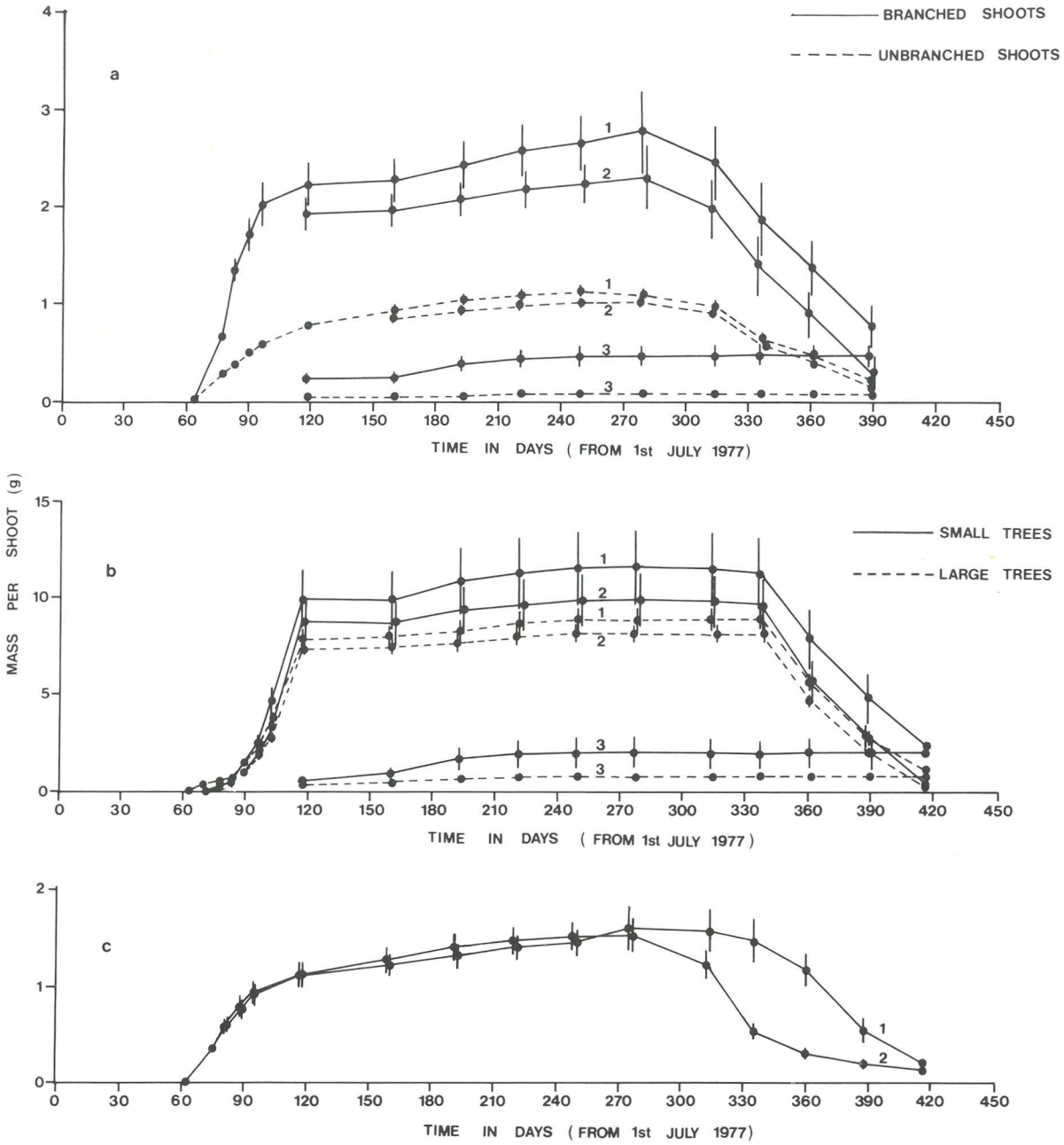

Figure 6 Comparison of seasonal change in shoot mass components between (a) branched and unbranched *Ochna pulchra* shoots and (b) small and large trees of *Burkea africana* in the main study season where 1 is shoot mass, 2 is leaf mass and 3 is twig mass. (c) Seasonal change in shoot mass showing two patterns of leaf mass reduction in *Ochna pulchra* in the main study season where 1 is for trees with greater than 5% of maximum leaf mass on day 390 and 2 is for trees with less than or equal to 5% of maximum leaf mass on day 390. 95% confidence limits are indicated.

branched versus 14% of the shoots in the lower half. The proportion of branched shoots was independent of plant size. In *Ochna pulchra* twig mass contributed 11% to the shoot mass and this proportion was unrelated to plant size. In *Burkea africana* the corresponding proportion was 12% but varied from 8% for the large plants (as defined above) to 18% for the small plants. In *Ochna pulchra* the proportion varied from 7% in unbranched shoots to 18% in branched shoots.

In *Ochna pulchra*, plants greater than 3,5 m in height produced inflorescences, those less than 1,8 m produced none, while plants in the intermediate height range varied in inflorescence production. The dependence of inflorescence production on plant height was clearer in *Burkea africana*. All plants greater than 6 m in height or with a stem diameter greater than 230 mm produced inflorescences and those less than 5 m or less than 120 mm in stem diameter did not. Of the trees that flowered, 13% of the shoots were inflorescences (hapaxanthy) in *Ochna pulchra*. For the corresponding *Burkea africana* trees, 73% of the shoots produced inflorescences in addition to leaves (pleonanthy). The proportions of shoots that flowered were 6% for upper canopies and 16% for lower canopies in *Ochna pulchra*, but 79% and 63% respectively in *Burkea africana*. No consistent relationship between number of inflorescences and number of leaves per shoot was found in *Burkea africana*.

Other study seasons

In the first season (1976/77) shoot growth started approximately ten days earlier than in 1977/78 (main season) in *Ochna pulchra*, whereas in *Burkea africana* shoot growth

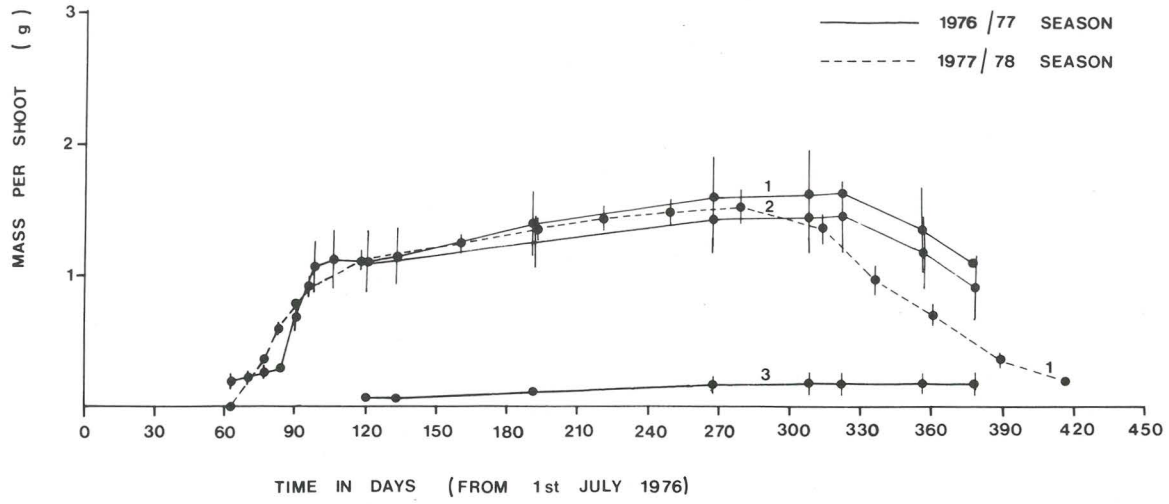

Figure 7 Seasonal change in shoot mass components for *Ochna pulchra* in the first study season with comparison of shoot mass change with that of the main study season where 1 is shoot mass, 2 is leaf mass and 3 is twig mass. 95% confidence limits are indicated.

started at about the same time as in the main season. The main period of growth in both species was about eight weeks, that is, similar to that of the main study season. As in the main study season there was a similar increase of 42% after the first flush of growth owing to second flushes in *Ochna pulchra*. Shoot mass peaked at 1,63 g/shoot in *Ochna pulchra* and at 6,48 g/shoot in *Burkea africana*. Although the pattern of shoot mass increase in *Ochna pulchra* was very similar in the 1976/77 and 1977/78 seasons, shoot mass started to decrease about six weeks later in the 1976/77 study season (Figure 7). In *Burkea africana* there was no difference in the pattern of decrease in shoot mass. The proportion of leaf and twig mass in the first season was similar to that in the main study season.

In the third study season (1978/79) shoot mass after the main period of growth was 1,46 g/shoot in *Ochna pulchra* and 7,81 g/shoot in *Burkea africana*. The proportion of leaf and twig mass remained unchanged. In the fourth study season (1979/80) shoot mass after the main period of growth was 1,14 g/shoot in *Ochna pulchra* and 7,21 g/shoot in *Burkea africana*. In *Burkea africana* the proportion of leaf and twig mass remained unchanged but in *Ochna pulchra* twig mass contributed only about 6% to the shoot mass in the last season.

Interseasonal growth

Shoot mass comparisons between different seasons are expressed in terms of a percentage incremental difference of the vegetative shoot mass in each preceding season. This percentage was calculated by $[(x - y)/y]$ 100 where x is current season's mass and y is previous season's mass. Comparisons can therefore be given for only the main and following two seasons. In *Ochna pulchra* for the second, third and fourth study seasons respectively, shoot mass changes were +17%, +36% and −9% and for *Burkea africana* were +107%, +9% and +26% respectively. Shoot numbers increased at a fairly constant rate in *Ochna pulchra* but shoot mass of *Ochna pulchra* and both shoot numbers and mean shoot mass in *Burkea africana* varied greatly with season. Part of the bud mass of the previous seasons is included in the shoot mass of the following seasons. Winter mean bud mass was 0,026 g in *Ochna pulchra* and 0,096 in *Burkea africana*. A linear dependence of percentage incremental difference in shoot mass on percentage deviation of the previous season's rainfall from the mean annual rainfall was found for *Ochna pulchra* (Figure 8). In *Burkea africana* there was no such relation

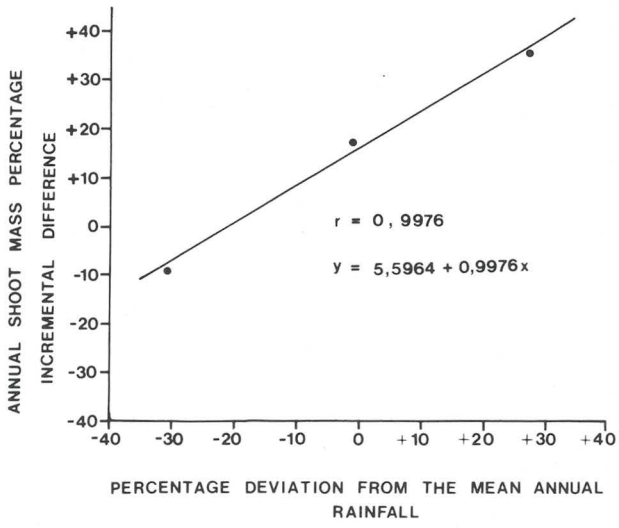

Figure 8 Relationship between percentage deviation from the annual rainfall mean at t and annual shoot mass percentage incremental difference at $t + 1$ for *Ochna pulchra* where t is years and r is correlation coefficient.

but the incremental difference in shoot mass did relate to the previous season's late rainfall in autumn (Figure 9). This relation improved marginally with the inclusion of rainfall in winter. *Ochna pulchra* shoot growth did not relate to the rainfall of autumn and winter preceding the new growth season.

The proportion of branched, unbranched and inflorescence shoots in *Ochna pulchra* are given for each study year in Table 1. In *Burkea africana* the proportion of shoots that produced inflorescences was consistently higher than that of *Ochna pulchra* in the first three study years, namely 22%, 54% and 14% respectively.

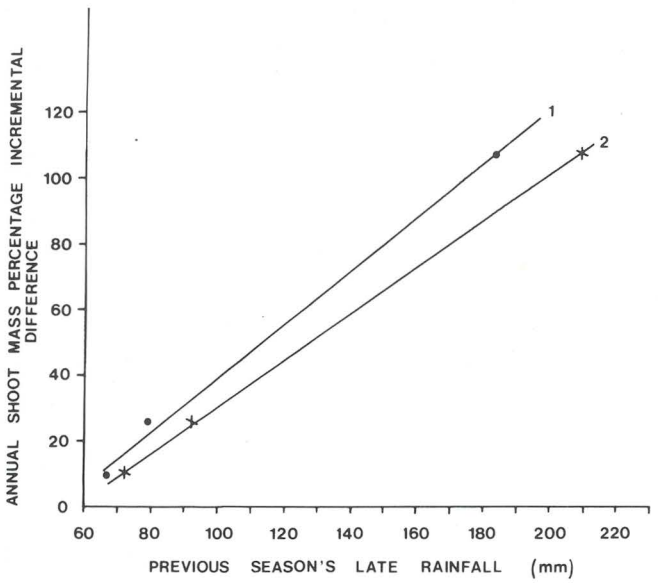

Figure 9 Relationship between previous season's late rainfall and annual shoot mass percentage incremental difference for *Burkea africana* where 1 is for autumn and $y = -42{,}7531 + 0{,}8205\,x$ and $r = 0{,}9976$ and where 2 is for autumn and winter and $y = -41{,}0541 + 0{,}7109\,x$ and $r = 0{,}9996$. (r is correlation coefficient.)

The fate of individual branched and unbranched shoots from one season to the next is given for *Ochna pulchra* in Table 2. Unbranched shoots tended to produce either unbranched or branched shoots the following year whereas branched shoots had the option of producing combinations of shoot types, the most common of which was the branched/unbranched combination. Branched shoots produced a greater proportion of unbranched shoots than branched in one season whereas unbranched shoots produced more of their own kind in both given seasons.

In *Ochna pulchra* a greater proportion of unbranched shoots died between seasons than did branched shoots (Table 2). In the same two periods, the proportions of dead shoots in *Burkea africana* were considerably lower than in *Ochna pulchra*, namely 5,5% and 9,4% respectively. In both *Ochna pulchra* and *Burkea africana* the death rate of shoots was higher between the last two seasons.

Table 1 The proportion of unbranched, branched and inflorescence shoots for each study year in *Ochna pulchra*

Year	% Unbranched	% Branched	% Flowering
1976/77	39	47	14
1977/78	69	23	8
1978/79	49	41	10
1979/80[a]	72	28	–

[a] Percentage of vegetative shoots only.

Leaf area

Specific Leaf Area in *Ochna pulchra* decreased rapidly from greater than 150 cm^2/g in the second week of growth to between approximately 80 and 70 cm^2/g after the eighth week of growth in the main study season (Figure 10). The Specific Leaf Area of *Burkea africana* decreased earlier than that of *Ochna pulchra* and stabilized at a sligtly lower level between approximately 70 and 60 cm^2/g. Direct measurements of leaf area in *Burkea africana* in the first study season (Figure 11) confirm the rapid cessation of leaf growth after the period of major growth. The first measurable point (Figure 11) with the cited apparatus was possible only after more than 60% of the leaf area had already expanded. Changes in leaf area generally followed changes in leaf mass for most of the period of seasonal leaf duration.

Discussion

The main period of active shoot growth with the associated production of flowers found in the present study, cor-

Table 2 Interseasonal fate of shoot types in *Ochna pulchra* (percentages of numbers of shoots)

		Shoot types								
Original shoot type	Period	unbranched only %	branched only %	inflores-cense only %	whole vegetative shoot death %	total terminated shoots %[a]	unbranched with branched %	unbranched with inflores-cence %	branched with inflores-cense %	unbranched with branched with inflorescense %
Unbranched	1977/78 to 1978/79	42	30	13	14	27	1	1	0	0
	1978/79 to 1979/80	57	11	b	b	31	1	0	0	0
Branched	1977/78 to 1978/79	16	22	3	6	9	46	1	4	2
	1978/79 to 1979/80	34	17	b	b	19	29	0	1	0

[a] Sum of the two preceding columns.
b = Data unavailable owing to later date of sampling

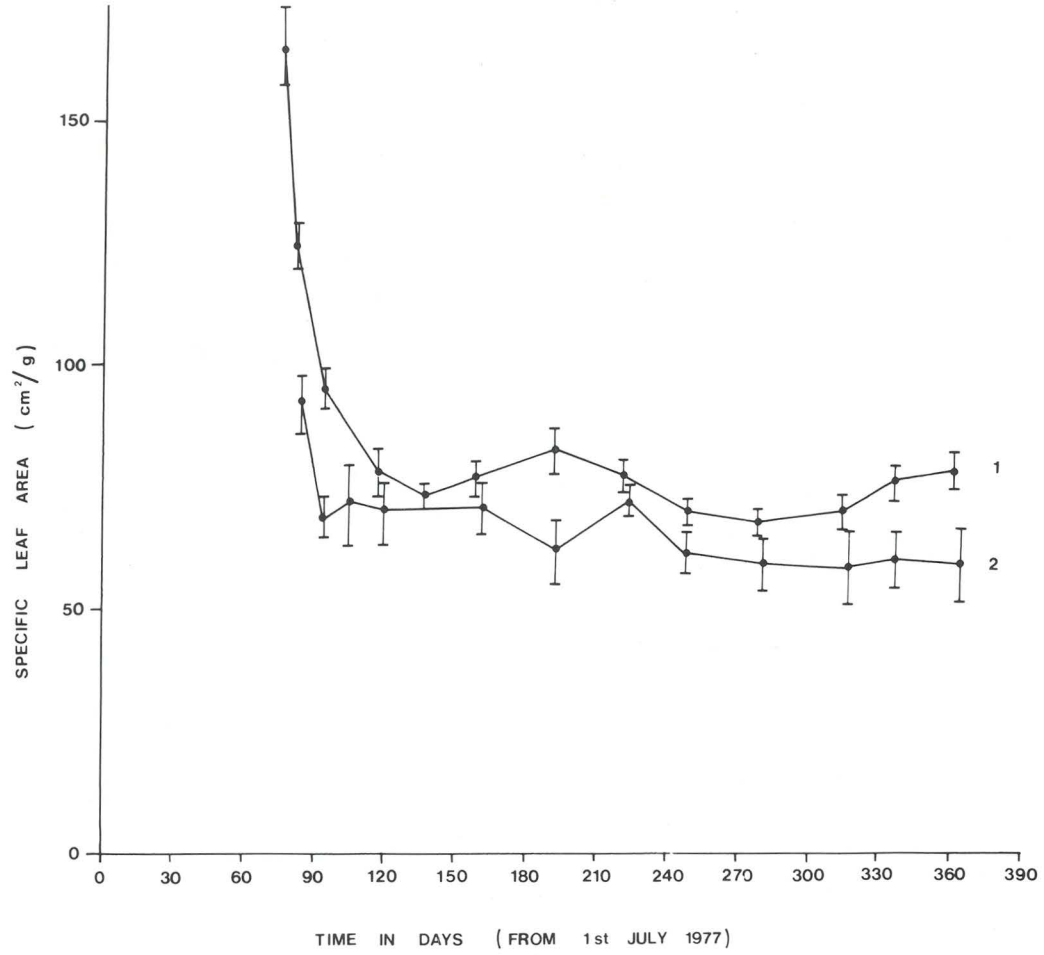

Figure 10 Seasonal progression of Specific Leaf Area for (1) *Ochna pulchra* and (2) *Burkea africana* in the main study season. 95% confidence limits are indicated.

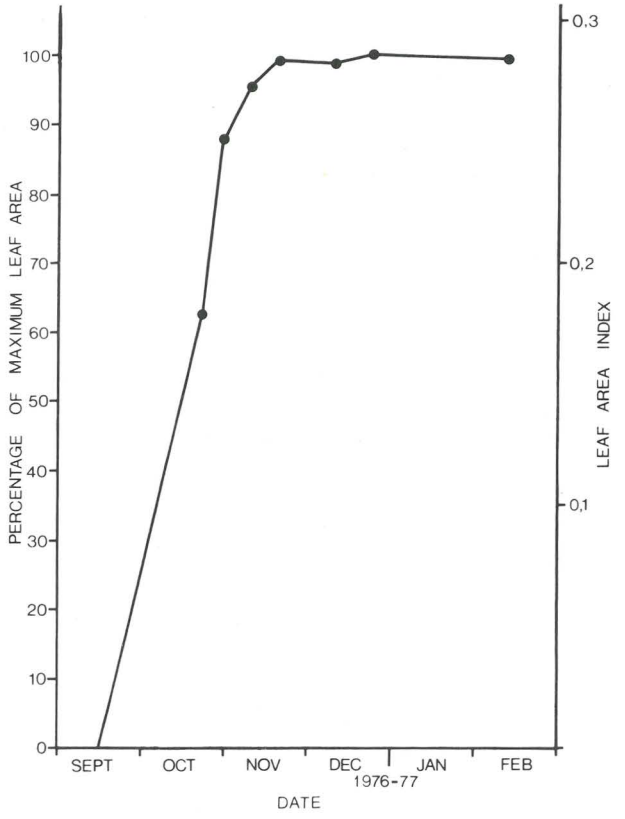

Figure 11 Seasonal progression of leaf area and Leaf Area Index (scaled to peak season's Leaf Area Index — Rutherford 1979a) for *Burkea africana* in the first study season.

responds well to the main period of tree flowering found in the warm dry season (August – September) in southern Zaire's miombo woodland (Malaisse 1974). Flowering in *Burkea africana* in the present study coincides with the September – October period recorded for this species in Tanzania (Boaler 1966), South West Africa/Namibia (Rutherford 1975) and (also for *Ochna pulchra*) herbarium specimen localities in southern Africa (Figure 12).

That variation in leaf initiation was generally less variable than that of the timing of leaf fall, pointed to a possible dependency of leaf initiation on the less variable seasonality in, for example, temperature increase and a dependency of leaf fall on the more variable seasonal rainfall. Various research results concerning northern hemisphere trees, quoted by Kozlowski (1964), support the associations between shoot growth initiation and increased temperature and between main period of shoot growth and greatest differences between day and night temperatures. The earlier initiation of *Ochna pulchra* shoot growth in the 1976/77 season relative to that in the 1977/78 season corresponds to a significantly higher (P = 0,01) daily range of temperature for the first three weeks of August in the first season. The growth curves determined in this study are not a standard sigmoid form because all buds within the canopy and plant population do not open simultaneously and have different lag times. Kozlowski (1964) confirms similar drawbacks to the idealized sigmoid curve in other tree species.

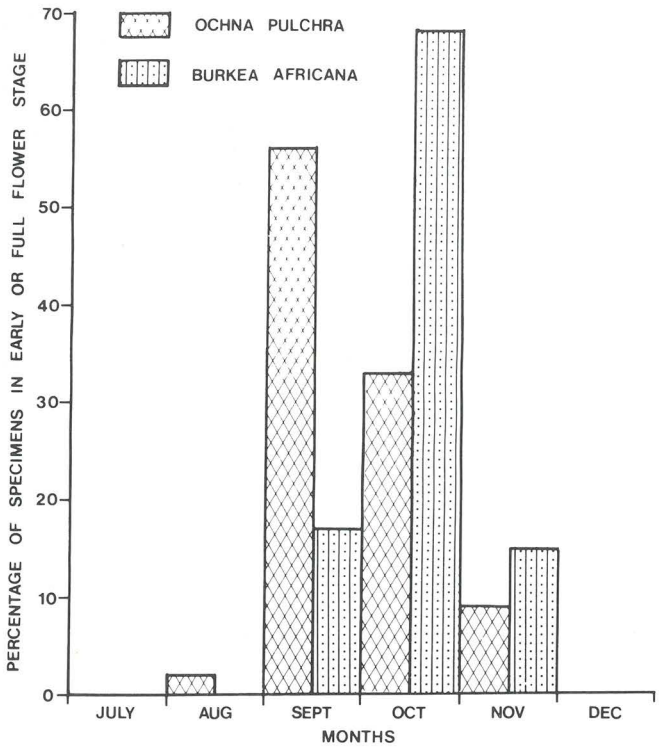

Figure 12 Monthly distribution of fully documented specimens in early or full flowering stage for *Ochna pulchra* and *Burkea africana* in southern Africa. (Old flower or early fruiting stages excluded.) Source: National Herbarium, Pretoria.

The average time of leaf fall in the study species on the Nylsvley site was usually earlier than the period of maximum leaf fall in August and September reported for high rainfall, southern Zaire miombo vegetation (Malaisse *et al.* 1975). The longer duration of leaves on trees of *Burkea africana* following above-average rains has been paralleled in South West African/Namibian savanna where most leaves on trees of this species were retained into August following a particularly high rainfall season (Rutherford 1975). The later retention of leaves in *Burkea africana* than in *Ochna pulchra* following above average rains, although possibly also temperature influenced, probably relates more closely to findings on the Nylsvley site (Moore 1980) that water uptake occurs throughout the soil profile in *Burkea africana* subhabitats but mainly from the top 600 mm in *Ochna pulchra* subhabitats. This difference in water uptake pattern corresponds with the generally deeper rooting system of *Burkea africana* relative to that of *Ochna pulchra* (Rutherford, in press). *Ochna pulchra* also developed lowest water potential values (more negative) of -4000 kPa during a period of extreme stress in the main study season compared to *Burkea africana* with a corresponding value of -3300 kPa. Throughout the season, *Ochna pulchra* appeared consistently less able to control water loss as efficiently as *Burkea africana* (Ferrar 1978). This may reflect a less effective morphological adaptation for water conservation in *Ochna pulchra* where there are large sunken stomata but no leaf surface hairs present, whereas in *Burkea africana* surface hairs and waxy deposits occur (Ferrar 1978). Ferrar indicates that within a season, leaf aging effects on photosynthesis in the two species can be overridden by increased soil water through rainfall but the exact limits are unknown. Although it is possible that the differences described above between *Ochna pulchra* and *Burkea africana* may be consistent, in their response to rainfall, it appears from data from the 1976/77 and 1977/78 seasons that variation in leaf fall within *Ochna pulchra* from year to year depends on factors other than rainfall.

The association of the second shoot growth flush with a gradual increase in the mass of some shoots probably relates mainly to secondary thickening of the twig tissues in *Ochna pulchra* but possibly to an extension of the new buds in the last half of the season in *Burkea africana*. Dostál, quoted by Longman (1978), has suggested that plants with an increased proportion of root material are better able to produce several shoot growth flushes in a growing season. That the magnitude of the second flush was greater in *Ochna pulchra* than in *Burkea africana* may, therefore, be linked to the higher proportion of below-ground mass found in *Ochna pulchra* (Rutherford, in press).

The end of the period of gradual increase in shoot mass corresponds to the April termination of photosynthesis found in the main study year in both *Ochna pulchra* and *Burkea africana* (Ferrar 1978). There may therefore be a period in which green leaves remain on the tree without photosynthesizing significantly. In this period, mass loss of various parts of the plant can, presumably, be expected owing to respiratory activity associated with pre-dormancy metabolic needs of the plant. Leaf resistances of less than 5 s/cm were recorded for both species at the start of this period (Ferrar 1978).

The growth of a shoot unit of both study species occurs over two growing seasons. In the first season the bud or primordial shoot system is formed. In the second season the bud opens and the shoot system expands. These 'fixed growth' shoots have the expected (Kramer & Kozlowski 1979) relatively short period of active growth in the second season. In *Ochna pulchra* and *Burkea africana* the proportion by mass of that part of the shoot (with bud scales) formed in the first season was between 1 and 2%. Kozlowski (1964) has pointed out that the amount of shoot growth often bears a close relation to bud size which is determined in the previous growth season. The recognition of shoot growth as a two-stage, biennial process is important in understanding the apparent relation found between shoot growth and part or all of the previous season's rainfall and not the rainfall of the season of shoot expansion. It has been shown in some other studies (for example on *Pinus* species — Kozlowski 1964) that increased precipitation during a growing season was reflected in increased shoot elongation the following year (although these results are by no means universal). Maximum gross photosynthesis determinations ($^{14}CO_2$ uptake) on the same site in the main study season (Ferrar 1978) indicated photosynthetic levels in *Ochna pulchra* and *Burkea africana* to be low (less than 8 ng cm^{-2} s^{-1}) during the main period of shoot expansion. Higher photosynthetic levels were typical only of the period following main shoot expansion. Findings such as the above, point to shoot growth depending primarily on carbohydrate reserves and not on current photosynthate. This notion is reinforced by the observation that shoot growth often commences before the first

rains of the season. Most of the shoot growth is completed before the start of the main part of the rainy season and before completion of seasonal growth of roots and the other aboveground parts of the plant (Rutherford *et al.* 1980). The present data suggest that increased interseasonal shoot mortality in both *Ochna pulchra* and *Burkea africana* may be a climatic response to previous season's drought.

The large difference in levels of flowering shoots in *Ochna pulchra* and *Burkea africana* may be related to inherent differences in organization of bud types. Trees of *Burkea africana* can afford to flower to a greater extent than those of *Ochna pulchra*. *Burkea africana* has pleonanthic shoots whereas *Ochna pulchra* has determinate, hapaxanthic shoots where flowering shoots do not normally continue growth in the following season (see Hallé *et al.* 1978). The relatively lower mortality of the pleonanthic shoots of *Burkea africana* explains, in part, the greater interseasonal relative growth of vegetative shoots in *Burkea africana* than in *Ochna pulchra* plants. Although the much higher maximum rates of photosynthesis found in the main study season in *Burkea africana* (63 ng cm^{-2} s^{-1}) than in *Ochna pulchra* (20 ng cm^{-2} s^{-1}) (Ferrar 1978) may be suggestive, these are difficult to relate to shoot production owing to the unknown day and night respiratory rates.

Syllepsis is reported to be a predominantly tropical phenomenon (Tomlinson 1978) and the increased variation found in the mass of branched shoots of *Ochna pulchra* is probably owing to different numbers of sylleptic branches on the same shoot. The proportion of branched and unbranched shoots in *Ochna pulchra* is important as it affects the rate and amount of shoot growth on a tree. For example, for a given number of shoots on a tree, a low proportion of branched shoots can be used to predict a reduced rate of shoot growth for the whole plant. The tendency for plants of *Ochna pulchra* to have a greater proportion of larger (branched) twigs in the upper half of the canopy possibly relates to the reduced shading of leaves in the upper half of the fairly dense canopies of this species. In *Ochna pulchra*, depth of canopy layers of individual plants on site are typically twice that for *Burkea africana* (Harrison, pers. comm.). The present data cannot support a similar statistical difference in vertical shoot mass distribution in *Burkea africana* trees owing to the limited depth of the flat canopies. However, the occurrence of larger twigs, commonly observable at the top of the canopy is likely to be ascribed to apical dominance (or more correctly 'apical control' in woody plant canopies — Brown *et al.* 1967) than to a differential shading effect in the generally open canopies. The larger shoots of the upper parts or top of canopies correspond to the 'long shoots' as apposed to the 'short shoots' in branch polymorphism (Hallé *et al.* 1978). These larger shoots consequently may be expected to play an important part in contributing to the future, main structure of the canopies.

The decreased individual shoot mass in the larger *Burkea africana* trees obeys one of Corner's (1949) principles, namely the 'Diminution on ramification' where the greater the ramification of branches in the tree, the smaller the branches and their appendages become. The same phenomenon is in keeping with the general plant age dependent patterns of shoot growth of Borchert (1976). However, the suggested decrease in sylleptic shoots in larger (older) trees was not found in *Ochna pulchra*. Borchert's (1976) observations may accord with the reduced magnitude of second flushes in *Burkea africana* (with larger and older trees) relative to those in *Ochna pulchra* (with generally smaller individuals) although this is a cross species comparison. Earlier initiation of leaf drop in smaller than in larger plants of *Ochna pulchra* does apparently not correspond to Kozlowski's (1973) quoted observation that leaves of adult trees usually abscise earlier in the year than leaves of juvenile plants. The leaf drop timings in *Ochna pulchra* do not appear to be affected by the possibly higher resilience associated with the often interconnected below-ground organs in smaller plants of *Ochna pulchra* which also have a higher ratio of below- to aboveground mass than the larger trees (Rutherford, in press). The phenomenon may be explained by possibly less effective water uptake in younger root systems of *Ochna pulchra* and the greater exposure of leaves of smaller plants to lower temperature minima nearer the ground. Night time temperature inversions have been recorded between 1 and 2 m height levels in a patch of *Ochna pulchra* in April (Harrison, pers. comm.).

The contributions of twig mass to shoot mass in *Ochna pulchra* and *Burkea africana* usually corresponded closely to those determined previously, more extensively on the study site (Rutherford 1979a). This helps suggest that the shoot sampling in the present study was representative of the populations for the whole study site. Only following the season of below average rainfall did the twig mass contribution to shoot mass decrease by about half in *Ochna pulchra*. Woody twig material of *Ochna pulchra* shoots appears, therefore, more sensitive to drought than the leafy material but this was not found in *Burkea africana* shoots.

The problem in obtaining monotonically increasing curves for shoot mass in the early stages of growth through use of regression analyses, appears intrinsic. Apart from the greater variability in the magnitude and initiation of shoot growth at the beginning of the season, two methodological artifacts are common. These are caused by the morphological preclusion of use of better shoot dimension estimators of mass at an early stage of growth, as well as the need to include other parameters, as the initial shoot parameters' ability to predict mass 'decays' with time. Although many smoothing techniques are available, their possible application here may be more aesthetic than informative.

The present study clearly illustrates certain limitations of the current approach in providing an adequate understanding of many field-recorded shoot growth phenomena. For more complete explanation of the role of climatic determinants in shoot growth as observed solely under natural ecological conditions, there is an uncomfortable need to rely on adequate chance variations in climate occurring from year to year. (In this respect, the present study was fortunate.) For adequate replication there is a further need for measurements over a period probably in excess of 10 or 15 years. The period of recording may need to be longer still if shoot growth data are to account for effects of recruitment and death of whole plants in the population. Various experimental approaches may provide the only short-term solution for obtaining a fuller

understanding of the dynamics of shoot system components.

Acknowledgements

The assistance of Messrs P.S. Carr and P. Phahlamohlaka at various stages in this work is gratefully acknowledged.

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